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Modelling the impact of climate change on Tanzanian forests

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Abstract

Aim: Climate change is pressing extra strain on the already degraded forest ecosystem in Tanzania. However, it is mostly unknown how climate change will affect the distribution of forests in the future. We aimed to model the impacts of climate change on natural forests to help inform national-level conservation and mitigation strategies.

Location: Tanzania.

Methods: We conducted maximum entropy (MaxEnt) modelling to simulate forest habitat suitability using the Tanzanian national forest inventory survey (1,307 occurrences) and environmental data. Changes in forest habitats were simulated under two Representative Concentration Pathways (RCPs) emission scenarios RCP 4.5 and RCP 8.5 for 2055 and 2085.

Results: The results indicate that climate change will threaten forest communities, especially fragmented strips of montane forests. Even under optimistic emission scenario, the extent of montane forest is projected to almost halve by 2085, intersecting many biodiversity hotspots across the Eastern Arc Mountains. Similarly, climate change is predicted to threaten microhabitat forests (i.e. thickets), with losses exceeding 70% by 2085 (RCP8.5). Other forest habitats are predicted to decrease (lowland forest and woodland) representing essential ecological networks, whereas suitable habitats for carbon-rich mangroves are predicted to expand by more than 40% at both scenarios.

Conclusions: Climate change will impact forests by accelerating habitat loss, and fragmentation and the remaining land suitable for forests will also be subject to pressures associated with rising demand for food and biofuels. These changes are likely to increase the probability of adverse impacts to the country's indigenous flora and fauna. Our findings, therefore, call for a shift in conservation efforts, focusing on (i) the enhanced management of existing protected areas that can absorb the impacts of future climate change, and (ii) expanding conservation efforts into newly suitable regions through effective land use planning and land reclamation, helping to preserve and enhance forest connectivity between fragmented patches.

KEYWORDS
Biodiversity conservation, climate change, conservation planning, habitat fragmentation, habitat suitability modelling, MaxEnt modelling, Tanzania

1 | INTRODUCTION

Tropical forests form the most abundant terrestrial reservoir of carbon storage and biodiversity (Newmark, 2006), but have experienced climate change impact, deforestation and habitat fragmentation (Bonan, 2008; Gibbs et al., 2010). The projected increase in global mean temperature of $4.3 \pm 0.7\ ^0$C by 2,100 for RCP8.5 is likely to affect further the geographical distribution, composition and productivity of tropical forest ecosystems (IPCC, 2014) adversely affecting vital ecosystem services. Sub-Saharan Africa has been identified as one of the most vulnerable parts of the world to the effects of climate change (Chidumayo, Okali, Kowero, & Larwanou, 2011; Serdeczny et al., 2016). Climate change is predicted to increase hazards such as flood and fire hazard, disease, food insecurity and habitat degradation (Serdeczny et al., 2016).

The effects of climate change on African tropical forest habitats mostly results from changes in precipitation patterns (particularly the influence of the El Niño-Southern Oscillation (ENSO)) (Butt et al., 2015) and the Subtropical Indian Ocean Dipole (SIOD)) and subsequent effects on soils and groundwater availability (Müller, Waha, Bondeau, & Heinke, 2014), alongside increases in atmospheric availability of CO_2 concentration and nitrogen deposition (Serdeczny et al., 2016). Even though the effect of climate changes has already been felt, its impact on the tropical forests remains relatively understudied (Delire, Ngomanda, & Jolly, 2008; Markham, 1998; Pacifici et al., 2015). This is mainly in resource-poor sub-Saharan Africa, where data are scarce, creating a barrier to incorporating climate change scenarios into land management and conservation planning (Lee & Jetz, 2008).

Increasingly, global initiatives and commitments are considering African tropical forests as critical components of climate change mitigation strategies such as the Bonn Challenge on Forest landscape restoration (FLR) (Seidl et al., 2017), the United Nations Framework Convention on Climate Change (UNFCCC) on reducing emissions from deforestation and forest degradation (REDD+) (Romijn, Herold, Kooistra, Murdiyarso, & Verchot, 2012), the Rio + 20 land degradation neutrality (Grainger, 2015), Aichi Target 15 on the restoration of degraded ecosystems (Tobón et al., 2017) and the 2030 agenda of the United Nations for Sustainable development goals (SDGs) 13 and 15 (Swamy, Drazen, Johnson, & Bukoski, 2017). To ensure that these strategies are successful and enable effective conservation, it is essential to establish a baseline in terms of forest habitat extent and resilience to climate change pressures (Clark, Gelfand, Woodall, & Zhu, 2014; Verdone & Seidl, 2017). This should be determined in a scalable and tractable manner, including modelling projections of future distributions to bridge the gap of data deficiency regarding sub-Saharan forests (Montagnini & Jordan, 2005).

Habitat suitability modelling (hereafter referred to as HSM) or species distribution modelling is widely applied in estimating changes in habitat suitability and counteract negative impacts of climate change (Edenius & Mikusiński, 2006; Lim et al., 2018; Title & Bemmels, 2017). It represents a valuable tool for informing policy-makers about the effects of climate change on forest community (Seidl et al., 2017). HSM focuses at identifying both the most influential environmental and climatic variables describing presence/absences, abundances or even growing conditions of forest species and the optimal relationships between their distributions and these explanatory variables (Jiménez-Alfaro et al., 2018). The provision of environmental and climatic variables from globally, often freely, available Earth Observation (EO) datasets enables simulations and subsequent information to be determined over scales that are suitable for national, regional and even global decision-making (Edenius & Mikusiński, 2006).

Maximum entropy (MaxEnt) modelling (Phillips, Anderson, & Schapire, 2006; Renner & Warton, 2013) has been used to successfully predict forest species habitat suitability under current and future climate scenarios for a range of sites across the world. For example, climate change impacts on forest habitat suitability and diversity in the Korean Peninsula (Lim et al., 2018); how much does climate change threatens European forest tree species distributions (Dyderski, Paź, Frelich, & Jagodziński, 2017); climate change impact on the distribution of Dipterocarp trees in Asia (Deb, Phinn, Butt, & McAlpine, 2017); induced range shift in miombo woodland due to climate change in Southern Africa (Pienaar, Thompson, Erasmus, Hill, & Witkowski, 2015). However, most of these studies are limited to a single-tree species, lacking multiple tree species (such as Edenius & Mikusiński, 2006; Jiménez-Alfaro et al., 2018; Rondinini, Stuart, & Boitani, 2005). In contrast, modelling multiple tree species tend to yield better results (Edenius & Mikusiński, 2006) as this approach relies on detecting the shared pattern of the environment response for sparsely recorded species, thereby simplifying intricate species-specific patterns. It also enables direct interpretation by decision-makers (Ferrier & Guisan, 2006) that would typically be at the community level, except for studies into particular threatened species (Brummitt et al., 2015).

Approaches like MaxEnt rely on the availability of species or habitat presence data, typically based on field observations of a particular species or habitat. In the United Republic of Tanzania, the National Forest Inventory (NFI) provides a comprehensive dataset that includes over 19 thousand observations of forest type with over 50 thousand points for dominant tree species over all ecological zones across the country (Minunno et al., 2019; Storch, Dormann, & Bauhus, 2018; Tomppo et al., 2014) providing an exciting opportunity to provide baseline maps of forests and woodlands extent and the subsequent influence of climate change (Lim et al., 2018).

This study uses MaxEnt to map the distribution of forest types in Tanzania centred on two climate Representative Concentration Pathways (RCPs) scenarios (RCP4.5 and RCP8.5) and the future period of 2055 and 2085. Specifically, we addressed the following research questions: (1) What are the vital climatic factors that affect the distribution of forest types based on dominant tree species in Tanzania? (2) What are the impacts of climate change on the distribution of the prevalent tree species habitats? (3) What are the implications for changes in the distribution of forest habitats on the conservation of globally significant indigenous flora and fauna?

2 | METHODS

2.1 | Study area

This study focused on the mainland United Republic of Tanzania (hereafter referred to as Tanzania) in East Africa (Figure 1). Tanzania's precipitation is characterized by bimodal rainfall distribution patterns ranging below 400 mm and over 2000 mm per year (Hardy et al., 2013). The maximum mean temperature ranges of 26.6–33.1°C and minimum at 5.3–18.3°C (NBS, 2017). The diverse geomorphological landscape results in a variety of climatic conditions, giving rise to a different set of forest communities (Table 1) from lowland rainforests in the north-west of the country to montane forests scattered across upland areas associated with the Eastern Arc Mountains (Burgess et al., 2004).

In Tanzania, forests (Figure 2 and Table 1) occupy an estimated 48.1 million hectares of land, equivalent to 55% of the total area (MNRT, 2015). Forests in Tanzania are rich in biodiversity and placed among the 36 global biodiversity hotspots (Hrdina & Romportl, 2017; Myers, Mittermeier, Mittermeier, Da Fonseca, & Kent, 2000). However, it is among the countries with the highest reported forest loss (Hansen et al., 2013) and high vulnerability to the effects of climate change (Montade et al., 2018; Platts, McClean, Lovett, & Marchant, 2008). Forests contribute significantly to rural life in Tanzania for food security, woody biomass for energy supply and household subsistence. Ecologically, forests help to conserve soil and water resources, harbouring genetic, functional and taxonomic diversity. Approximately 35% of forests are protected through forest reserves, national parks and game controlled areas. However, 75% of forests are found on unprotected, general-use land and are therefore vulnerable to degradation or deforestation, mainly due to growing need for agriculture and biofuel production, as well as extensive uncontrolled firewood collection, charcoal production, as well as the effects of forest fires (MNRT, 2015).

3 | DATASETS

3.1 | Forest occurrence data

Forest occurrence records were acquired from the National Forest Resources Monitoring and Assessment (NAFORMA) released in

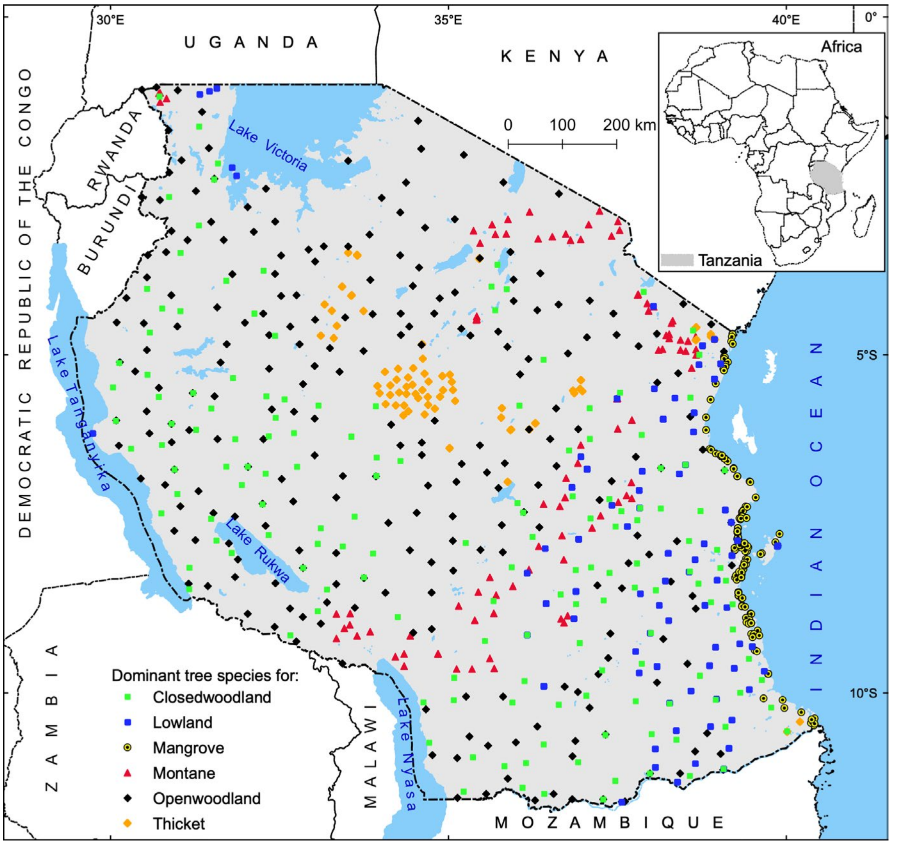

FIGURE 1 Study area with the distribution of the presence points for dominant tree species from natural forest types in Tanzania. EPSG: 4,326, WGS84 projection

TABLE 1 Descriptions and main characteristics of the forest types (Figure 1) in Tanzania (MNRT, 2015)

Forest types					
Level 1	**Level 2**	**Description**	**Altitude (m)**	**Crown cover (%)**	**Height (m)**
Forest	Montane	Catchment forests found in mountainous areas and changes with elevation	1400–1850	> 40	> 5
	Lowland	Include groundwater forest and mainly located near the coast of the Indian ocean and in small portion of the mixture with woodlands and montane forest	540– 810	> 40	> 5
	Mangrove	Grow on the upper part of the inter-tidal zone of the sheltered shores of the delta, alongside the river estuaries and the creeks, mainly along the Indian Ocean. May occur with other wooded land vegetation	≤ 25	> 40	> 5
Woodland	Closed woodland	Dominated with perennial C4-grasses which induce regular fire occurrences in the month of May to November before rain season	100–1400	> 40	> 5
	Open woodland	The same description as closed woodland with the difference in canopy cover	100–1400	10–40	> 5
Thicket	Thicket	Dense evergreen or deciduous thorn woodland. Grow interlocked and make impassable community	1244–1300	5–10	<5

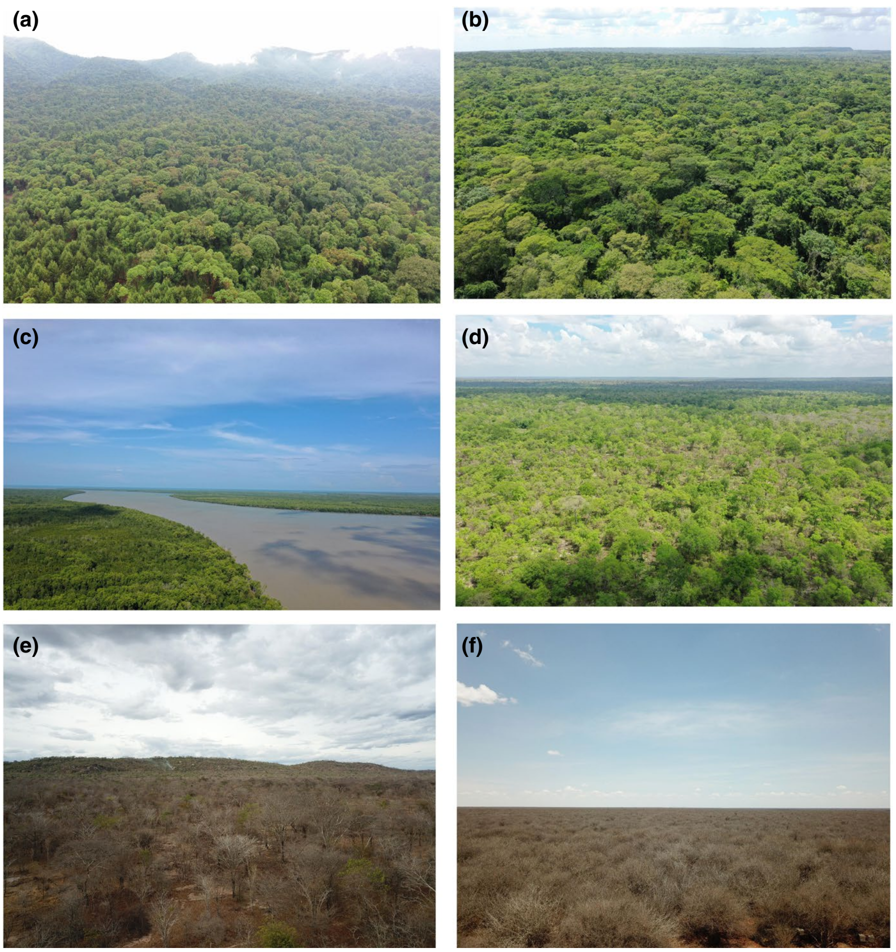

FIGURE 2 Aerial photographs for the natural forest types in Tanzania based on drone capture (height ~ 60 m), October 2019: (a) montane forest, (b) lowland forest (c) mangrove forest, (d) closed woodland, (e) open woodland and (f) thicket

TABLE 2 Summary statistical information for major predictor variables of forest types based on the occurrence data used in this study. Bio1: mean annual temperature; Bio12: mean annual rainfall; Bio14: rainfall driest month; Elv: elevation; Tri: terrain ruggedness index

Forest type	Scientific name of dominant trees	Code	Unit	Mean	*SD*	Min.	Max.
Montane	*Ekerbergis Capensis, Olea capensis, Albizia gummifera, Ocotea usambaraensis, Newtonia buchananni,*	Bio1	°C	17.01	0.10	10.40	26.10
		Bio12	mm	1,247.61	10.72	850.00	2,686.00
		Bio14	mm	14.80	0.64	0.00	66.00
		Elv	m	1,760	19	235	3,039
		Tri	m	92.11	1.94	8.38	229.88
Lowland	*Antiaris toxicaria, Scorodophloeus fischeri, Soriendea madagascariensis, Milletia stuhlmannii and Milicia excelsa*	Bio1	°C	24.72	0.04	15.00	27.30
		Bio12	mm	1,219.44	6.47	610.00	2,735.00
		Bio14	mm	11.20	0.33	0.00	56.00
		Elv	m	363.32	7.34	9.00	2,377.00
		Tri	m	36.40	1.20	1.12	279.25
Mangrove	*Avicennia marina, Sonneratia alba and Rhizophora mucronata*	Bio1	°C	26.69	0.04	25.90	27.50
		Bio12	mm	1,342.84	4.46	992.00	1869.00
		Bio14	mm	17.00	0.15	7.00	49.00
		Elv	m	8.82	0.08	1.00	22.00
		Tri	m	2.60	0.06	0.12	2,479.80
Closed woodland	*Brachystegia speciformis, Julbernardia globiflora, Brachystegia microphylla, Erythrophleum africanum and Burkea africana*	Bio1	°C	22.56	0.01	13.7	27.20
		Bio12	mm	1,139.84	1.16	556.00	2,377.00
		Bio14	mm	1.64	0.01	0.00	35.00
		Elv	m	1,040.06	2.00	14.00	2039.00
		Tri	m	29.96	0.16	0.38	248.12
Open woodland	*Combretum spp, Acacia spp, Commiphora spp, Lonchocarpus sp, Lannea spp and Terminalia spp*	Bio1	°C	22.97	0.01	13.90	27.30
		Bio12	mm	1,021.89	1.86	519.00	2,715.00
		Bio14	mm	3.59	0.04	0.00	48.00
		Elv	m	942.05	3.54	10.00	2,276.00
		Tri	m	22.88	0.21	0.25	231.12
Thickets	*Pseudoprosopis fischeri, Combretum celastroids and Dicrostachys cinerea,*	Bio1	°C	22.19	0.10	20.10	25.60
		Bio12	mm	766.08	11.45	566.00	1,243.00
		Bio14	mm	3.27	0.80	0.00	38.00
		Elv	m	1,160.47	28.57	106.00	1516.00
		Tri	m	8.78	0.67	2.38	45.38

2015. A total of 19,382 plots were measured between 2010 and 2014 containing 59,208 forest type points (dominant tree species) (MNRT, 2015). The dominant tree species are proxy indicators of habitat types for different existing forest types and dependent species (e.g. epiphytes of montane forests). Therefore, when dominant species change, this may impact connected species in the ecosystem. Hence, they provide long-term forest monitoring of habitat in response to climate change (Dyderski et al., 2017). The presence-only records were chosen based on abundance from the plot measurements for each forest type (Figure 2 and Table 1). The selection included both percentage frequency (occurrence) and abundance (proportional of individuals). This implies that only the most frequent and abundant species from each forest type were selected.

The plots consisted of 1, 5, 10 and 15 m radius concentric nested circular sub-plots, collected over a series of study clusters—L-shaped transects, consisting of six to ten plots with 250 m spacing between plots. The study clusters were distributed based on a double sampling for stratification approach (see Tomppo et al. (2014)) for full details of this procedure). The timberline species were excluded from the analysis as their habitat changes are mainly the result of different non-climatic anthropogenic drivers such as land management decisions (e.g. Bodin et al., 2013).

3.2 | Spatial rarefaction

Geographical bias in the habitat or species occurrence data is likely to result in model over-fitting and artificial inflation of model performance (Boria, Olson, Goodman, & Anderson, 2014; Veloz, 2009). Therefore, the original 59,208 forest type points underwent a stepwise spatial rarefication process, based on the random selection of a single location within grids of increasing size (Brown, 2014).

TABLE 3 Summary of predicted habitat suitability changes for the forest types (montane, lowland, mangrove, closed woodland, open woodland and thicket)

Pixel value			
Baseline suitability	**Future suitability**	**Predicted habitat suitability change**	**Description**
0	0	Unsuitable (no change)	Not suitable habitat at the current and future climate
0	1	Expansion (gain)	Not suitable habitat at the current climate but may be suitable in the future climate
1	0	Contraction (loss)	Suitable habitat at present but not in the future climate
1	1	Suitable (stable, no change)	Suitable habitat at both, current and future climate

TABLE 4 Model performance evaluation by AUC for the potential current distribution of forests using MaxEnt and a cloglog threshold for binary predictions. $AUC_{DIFF} = AUC_{training} - AUC_{testing}$

Forest type	AUC_{test}	AUC_{DIFF}	AUC_{SD}	Cloglog threshold
Closed woodland	0.72	0.056	0.082	0.425
Open woodland	0.60	0.068	0.079	0.479
Montane	0.96	0.003	0.014	0.245
Lowland	0.93	0.007	0.021	0.325
Mangrove	0.97	0.000	0.005	0.521
Thicket	0.92	0.012	0.039	0.183

Specifically, we created a 5 x 5 km fishnet grid over the entire extent, to produce a single distribution point selected in each grid, with at least the distribution points be at 5 km apart. It was performed for each forest category separately to avoid eliminating too many observations from less extensive forest types, such as mangrove and montane forests. This procedure resulted in the selection of 1,307 occurrence points ($n = 103$ montane, $n = 276$ lowland, $n = 168$ mangrove, $n = 378$ closed woodland, $n = 301$ open woodland and $n = 81$ thicket) that were considered to be spatially independent.

3.3 | Environmental variables

The selection of environmental variables was based on a conceptual model that encompasses factors deemed to control the presence, or in some cases, absence, of a particular species (Jiménez-Alfaro et al., 2018). In this instance, we based our variable selection on the parameters that control the physically based forest growth model 3-PG (Physiological Principle in Predicting Growth) (Landsberg & Waring, 1997; White, Scott, Hirsch, & Running, 2006). 3-PG includes a large number of parameters, but we limited our selection to those parameters listed in Appendix 1 as Table A2.

Current and future bioclimatic variables were obtained from the KITE dataset (AFRICLIM) (https://webfiles.york.ac.uk/KITE/AfriClim/ByCountry/Tanzania/) (Platts, Omeny, & Marchant, 2015). Future climate data were ensemble mean downscaled to the resolutions (~ 1 km) using 18 pairwise combinations of five regional climate models (RCMs) driven by 10 general circulation models (GCMs). A detailed explanation about data downscaling is found in Platts et al., (2015). The ensembles were projected under two RCPs (RCP4.5 and RCP8.5) based on the Fifth Assessment Report (AR5) of the United Nations Intergovernmental Panel on Climate Change (IPCC). It represents independent trajectories on emissions, socioeconomic and policy (Moss et al., 2010). RCP4.5 is an intermediate stabilizing pathway of the average 2041–2070 referred to as RCP4.5–2055, and it is the optimistic pathways without an overshoot scenario at 4.5 W/m^2 (~ 650 ppm CO_2 eq.) by 2,100 (Wise et al., 2009). It supports climate policies on reducing emissions, with moderate population and economic growth with reforestation programmes and increases areas of natural vegetation (Van Vuuren et al., 2011). RCP8.5 as a long term was the average of 2071–2100 referred to as RCP8.5–2085, and it is a pessimistic pathway with rising radiative forcing pathway leading to 8.5 W/m^2 (~1,370 ppm CO_2 eq.) by 2,100 (Moss et al., 2010). This scenario assumes no policy change to reduce emissions, with high population growth, low-income, increased energy demand and deforestation, especially in the least developed countries (Hurtt et al., 2011; Riahi et al., 2011).

Other variables selected included those relating to terrain and soil characteristics. The Shuttle Radar Topography Mission (SRTM) 1-arc second elevation data were obtained from USGS Earth Explorer to generate a terrain ruggedness index, a proxy measure of topographic heterogeneity (Riley, DeGloria, & Elliot, 1999). Soil characteristic variables were obtained from the World Soil Information (ISRIC) (https://www.isric.org) included soil types (see Appendix 1 as Table A1) (Hengl et al., 2015). A pairwise Pearson correlation (r) was used to test for collinearity between predicting variables, taking a relationship $r > 0.7$ or < -0.7 as highly correlated (Braunisch et al., 2013; Dormann et al., 2012) (see Appendix 1 as Table A3). Table 2 summarizes the general statistics of the selected bioclimatic and topographic profiles of forest types under current conditions based on the occurrence data used in this study.

3.4 | Forest modelling

The modelling process focused on forest types (Table 1, Figure 2) based only on dominant tree species (Table 2). The inventory data adequately presented the distribution of forest types at different compositional gradients to predict suitable habitats for both current and future climate. The approach involves modelling forest types independently and then ensemble the results (Ferrier & Guisan, 2006). In this manner, we can predict the distribution of forest types in a grouped way based on the trait characters (D'Amen, Rahbek, Zimmermann, & Guisan, 2017). The method follows the assumption that similar populations group have the same response to the environmental gradients based on the relative importance of environmental predictors (Rose, Kennard, Moffatt, Sheldon, & Butler, 2016).

3.5 | MaxEnt modelling and calibration

MaxEnt software version 3.4.1 (Phillips, Anderson, Dudík, Schapire, & Blair, 2017) was used to model forest types at the national scale. The data (occurrence and environmental data) were prepared using QGIS 3.6 version (https://www.qgis.org) and the Remote Sensing and GIS software library (RSGISLib; Bunting, Clewley, Lucas, & Gillingham, 2014; https://www.rsgislib.org/).

MaxEnt simulations were performed for each forest type using 50 replicates with 10,000 randomly sampled pseudo-absence points. The maximum number of iterations was set to 1,000, while the convergence threshold was defined at 0.001, to enable each replicate to converge within an acceptable time frame. Cross-validation was used to partition the 1,307 occurrence records for model calibration and evaluation purposes, whereby 75% of the occurrence records were used for model calibration while the remaining 25% retained for model validation. A regularization multiplier of one was used to limit model overfitting and enable the formulation of smooth response curves (Merow, Smith, & Silander, 2013). The log-log (clog log) output format was selected based on a sampling design that typically reflects the presence of localities and abundance of each forest type per quadrant at the presence probability of 0.63 (Phillips, 2005) and the location of occurrence is well estimated (Phillips et al., 2017). Jackknife resampling was used to examine the importance of each variable contribution to the potential distribution of vegetation types (Olivier, van Aarde, & Lombard, 2013).

3.6 | Construction of baseline and change maps

The final habitat suitability maps were generated by transforming the continuous probability values, ranged from 0 to 1 representing low and high probability, respectively, to discrete values of being either suitable or not suitable for the baseline. Following Spiers, Oatham, Rostant, and Farrell, (2018), the 10th-percentile training presence threshold was used to define suitable and unsuitable habitat for current and future projections. The future predicted habitat is calculated, for each forest type and taken as the difference between the baseline model and the future models to generate change maps (Maharaj & New, 2013) at RCP4.5 and RCP8.5, respectively, and presented with four predicted habitats of unsuitable, suitable, expansion and contraction (Table 3).

3.7 | Model performance evaluation

The models were evaluated using the qualitative statistic for the area under the curve (AUC) of the receiver operating characteristic (ROC) curves of the test data for the predicted mean accuracy model output for each forest type (Fielding & Bell, 1997; Merow et al., 2013). Model overfitting was quantified using $AUC_{DIFF} = AUC_{training} - AUC_{testing}$ (Warren & Seifert, 2011) with excellent model performance when AUC_{DIFF} is close to 0 (Bosso, Febbraro, Cristinzio, Zoina, & Russo, 2016).

3.8 | Baseline model accuracy assessment

AUC values have received criticism as they are vulnerable to over-inflation of model performance where spatial autocorrelation exists within the model variables and where a modelled habitat niche is small relative to the extent of the modelled area (Williams Cross, Crump, Drost, & Thomas, 2015). To alleviate these issues, we conducted an independent measure of model accuracy using the forest tree species data, removed during spatial rarefication process, including a total of 57,901 points. The agreement was quantified using three metrics: 1) overall % accuracy and associated confidence interval (CI) (Olofsson et al., 2014; Pontius & Millones, 2011), 2) F1 score index which depicts the harmonic mean among precision (p) and recall (r) for each class (Sofaer, Hoeting, & Jarnevich, 2019) and 3) Matthews correlation coefficient (MCC), which is explained in terms of true positive (TP), true negative (TN), false positive (FP) and false negative (FN) (Boughorbel, Jarray, & El-Anbari, 2017).

4 | RESULTS

4.1 | Model performance and habitat suitability estimation

Mean test AUC score demonstrated a high degree of accuracy (AUC > 0.9) for modelling the suitability of montane, lowland, mangrove forest and thicket (Table 4, Figure 3a-c, Figure 4). Closed woodland also showed a good level of accuracy (AUC = 0.72) (Table 4, Figure 5a). The relatively low standard deviation in AUC (ranged from 0.005 to 0.082) demonstrated a degree of model stability (Table 4). The model for open woodland calibrated inadequately (AUC = 0.6) (Table 4, Figure 5b). This result was expected since open woodlands are dynamic with unconstrained habitat niche, leading to a great deal of overlap with other forest

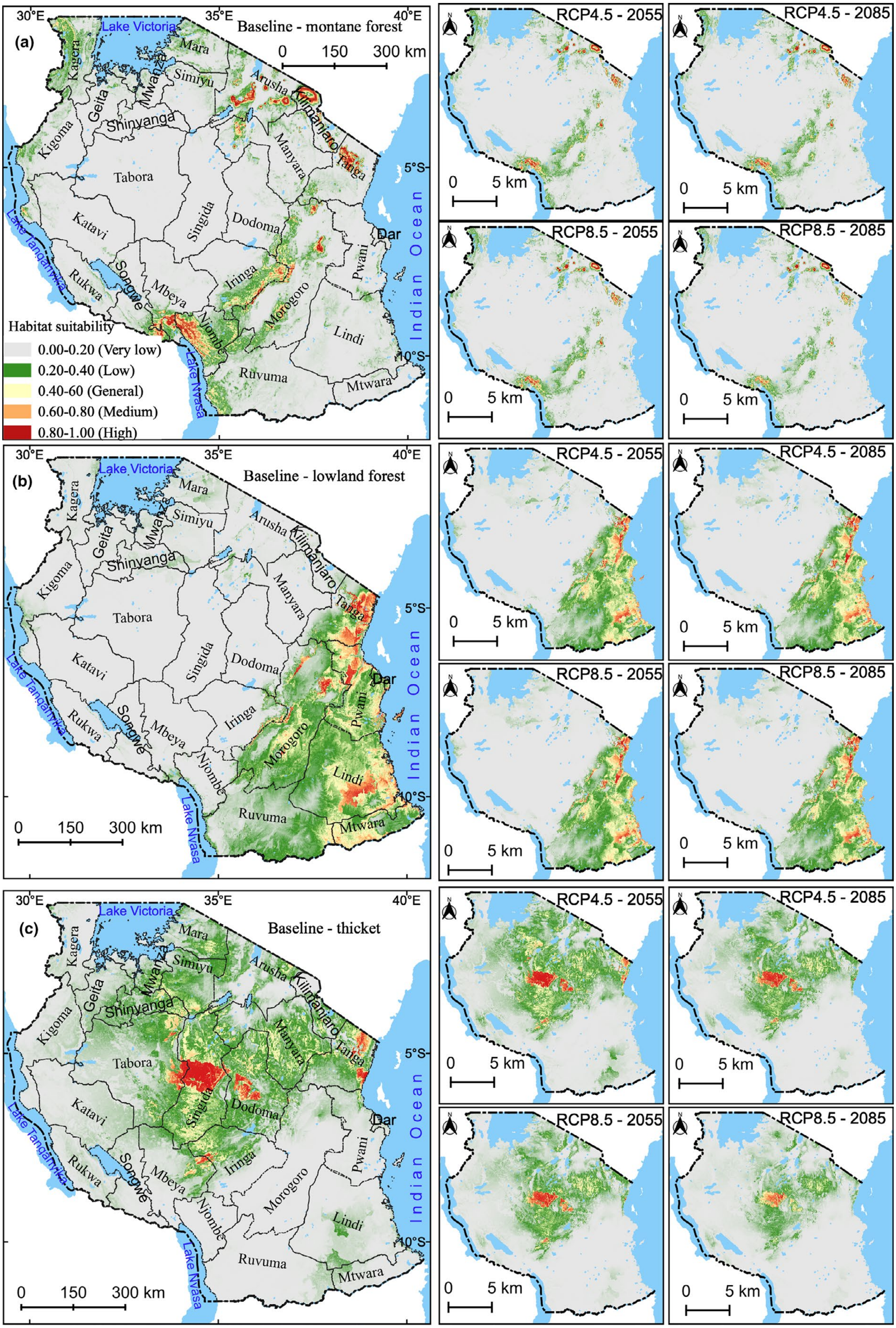

FIGURE 3 Predicted potential suitable habitat distribution area for (a) montane, (b) lowland forest and (c) thicket under current and future climate scenarios in Tanzania. EPSG: 4,326, WGS84 projection

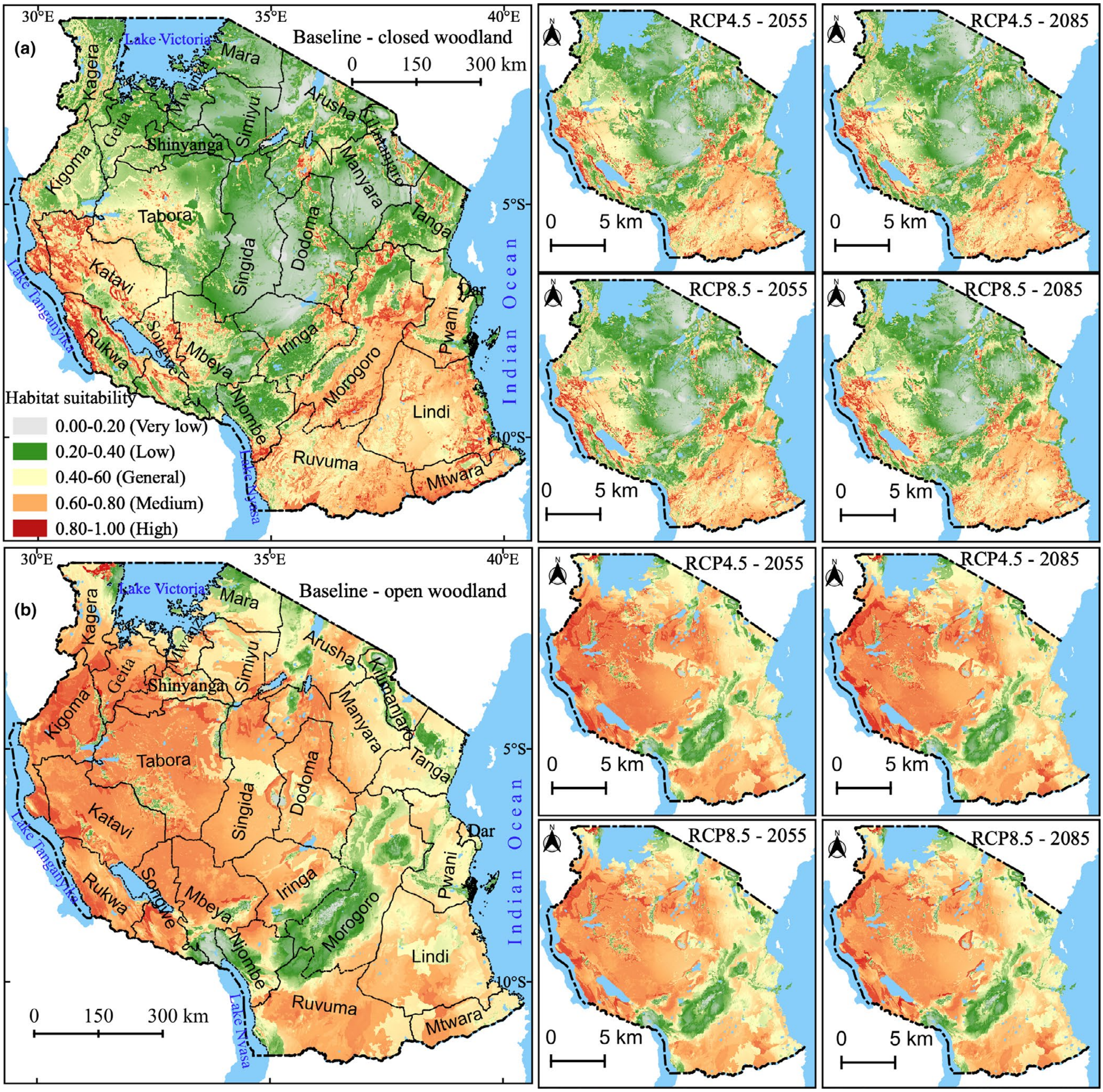

FIGURE 4 Predicted potential suitable habitat distribution area for mangrove forest under current and future climate scenarios in Tanzania (a) northern coastline of Tanzania (b) southern coastline of Tanzania. EPSG: 4,326, WGS84 projection

communities, especially closed woodland, lowland and thicket. The results of the accuracy assessment using independent dataset also indicated a good level of agreement. A mean overall accuracy of 90% ranging from 85% to 97%, F1 score of 0.9 (range of 0.84 to 0.98) and an MCC mean value of 0.83 ranging from 0.75 to 0.95 (Table 5) were attained. Therefore, the accuracy metrics indicated that the models are reliable to explain the potential habitats of the forest types and can adequately reflect their distribution in Tanzania in the present and future time. The main source of confusion occurred along the boundaries between forest types. These transitional zones rarely occur as sharp boundaries and are therefore likely to include a mix of forest types.

4.2 | Variables importance to each model

Precipitation and temperature (mean annual precipitation, rainfall driest month and mean annual temperature) (Table 6) were the main determinants for explaining the current and future distribution of the forest types in Tanzania. However, non-climatic variables reflecting

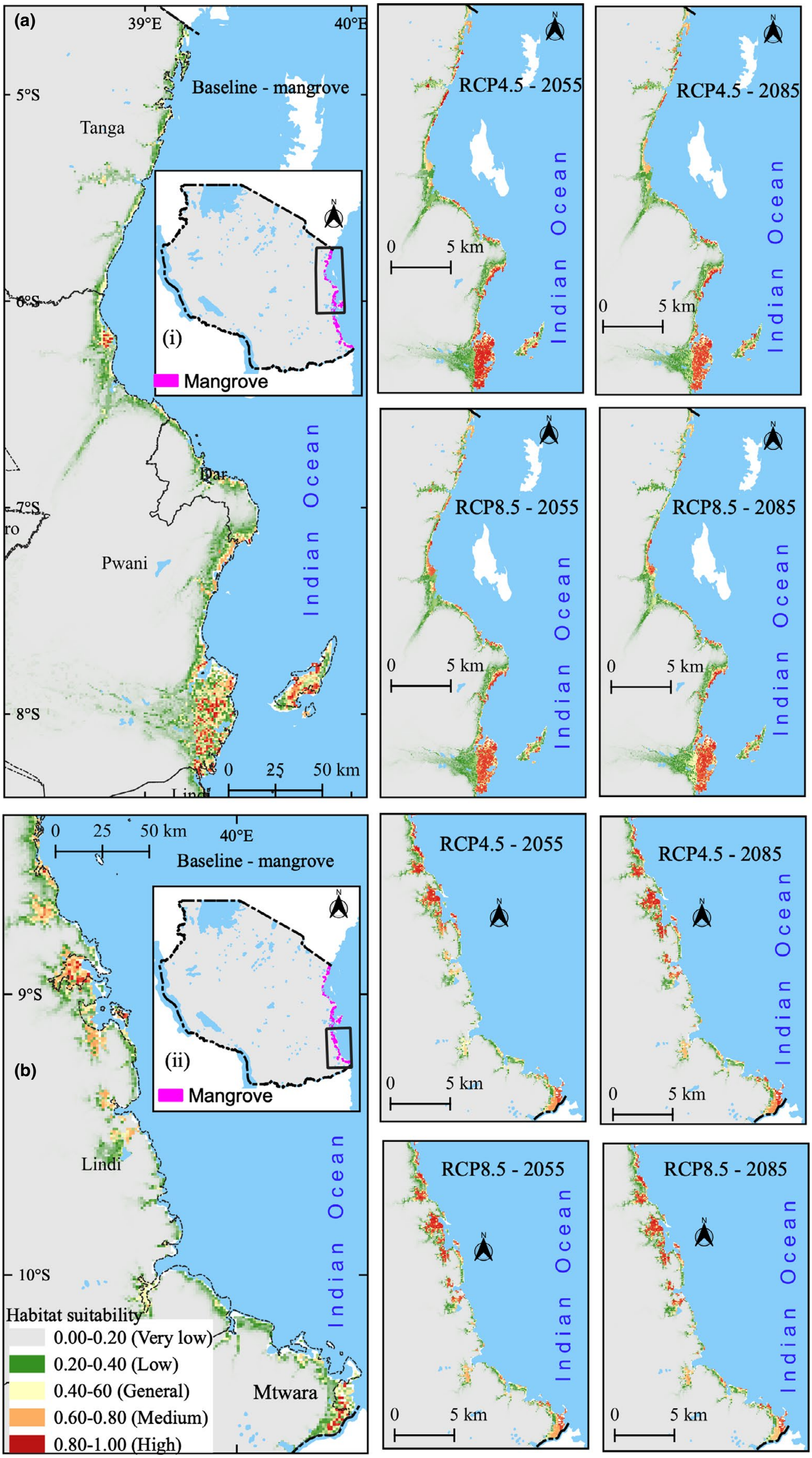

FIGURE 5 Predicted potential suitable habitat distribution area for (a) closed woodland, (b) open woodland and under current and future climate scenarios in Tanzania. EPSG: 4,326, WGS84 projection

TABLE 5 Summary of the accuracy metrics: overall accuracy, F1 score and MCC

Forest type	Overall Accuracy	F1 score	MCC
Montane forest	0.943 ± 0.014	0.93	0.88
Lowland forest	0.925 ± 0.010	0.92	0.85
Mangrove forest	0.976 ± 0.006	0.98	0.95
Closed woodland	0.879 ± 0.002	0.88	0.75
Open woodland	0.852 ± 0.003	0.84	0.77
Thicket	0. 894 ± 0.039	0.89	0.78

the topographic (elevation and terrain ruggedness) and soil constraints the distribution of these forest types, especially mangrove forest on the flat coastal plains. For example, removing elevation for the mangrove model resulted in a shift from the known areas of the mangrove occurrences to inland lakes and rivers.

4.3 | Predicted forests habitat distribution

The climate change scenarios indicate a projected change of suitable habitat for most forest communities (Tables 7 and 8). Montane forests, located on moderate-to-high altitude, are predicted to suffer a loss of more than 47% in suitable habitat extent by 2085 under even the most optimistic emission scenario (RCP4.5), and losses of 64% under a high emission scenario (RCP8.5). Thicket forests are predicted to lose more than 70% of its habitat under the high emission scenario (RCP8.5) by 2085. Mangrove forests are predicted to increase by 40% at both emission scenarios (RCP4.5 and RCP8.5). Lowland forest habitat, occurring in a mosaic with montane and woodland is predicted to have lost a suitable habitat of more than 10% by 2085 (RCP8.5). Woodland vegetation, the most geographically extensive forest type in Tanzania, is predicted to lose approximately 5% of its suitable habitat by 2085. Projected change maps (Figures 6, 7 and 8) present the anticipated changes in the forest suitable habitats from the projected baseline to the future climate in Tanzania.

5 | DISCUSSION

5.1 | Predicted forests habitat change

We assessed the impact of climate change on forests extent in Tanzania using national forest inventory data (Tomppo et al., 2014). Our results indicate that climate change will affect all forest habitats suitability across Tanzania. The results reveal that climate change will threaten forests at various scales: forests with a narrow geographical range occurring at high altitude (i.e. montane forests) will experience more loss of their current habitat in the future. This may be associated with fragmented strips of montane forests, and particularly high endemism has increased a great sensitivity to climate change (Foster, 2001). Moreover, future climate change will extensively threaten microhabitat forests (i.e. thickets) occurring in a semi-arid climate (Moncrieff, Scheiter, Slingsby, & Higgins, 2015). These projections indicate that climate change, especially temperature rise, will accelerate habitat loss of already vulnerable forests such as thickets (Chidumayo et al., 2011). Mangrove forests are predicted to expand their current range as a response to climate change (Godoy & Lacerda, 2015), although the future extent shift is more likely to be driven by sea-level rise, which was not factored, into the present study (Alongi, 2008).

5.2 | Potential suitable habitat impacted

The loss of suitable habitat for the montane forest is projected to be extensive, with losses exceeding 40% even under the optimistic RCP4.5 scenario by 2055 (Tables 7 and 8). This predicted loss is particularly pronounced in the high biodiversity areas of the Eastern Arc Mountains, a foothill of Rungwe and Livingstone mountain range along Lake Nyasa (Figure 6a). A projected reduction in rainfall results in a contraction of montane forests to higher elevations, illustrated by the projected loss of montane forest communities at lower elevations around Mount Kilimanjaro. The isolated nature of these montane habitats, sometimes termed "forest islands" (Fjeldså, 1999), form essential refugia for several species including 15 mammal species identified as vulnerable or high-risk status within the Udzungwa Mountains (Rovero et al., 2006). Forest loss in montane regions has severe implications for wildlife migration as these forests provide vital corridors linking reserves in Ruaha to the Selous Game Reserve via the montane forests of the Udzungwa Mountains (Jones et al., 2012). Additionally, loss of suitable habitat for forests in these regions is likely to increase sediment supply within the Rufiji basin, affecting downstream wetland dynamics and water resources (Ochieng, 2002).

Rising temperatures and reduced rainfall during the dry season are projected to result in losses of suitable lowland forest habitat above 10% by 2085 (Table 8). Given the extent of lowland forest in Tanzania, the effects of this loss have broad-reaching implications, including reduced landscape connectivity impacting wildlife migrations (Ntongani, Munishi, & Mbilinyi, 2010). Projected losses are particularly pronounced in the southeast of the country in the regions of Ruvuma, Mtwara and Lindi (Figure 6b), which provides an extensive trans-boundary wildlife corridor between the Selous and Niassa (Mozambique) game reserves. Lowland forest communities in this area mosaic with one of the World's largest miombo woodland ecosystems with a projected decline of above 4% (Tables 7 and 8) providing migratory routes for a number of species including the largest populations of elephants, as well as globally significant populations of Roosevelt's sable antelope, Liechtenstein's hartebeest, Nyasa wildebeest, eland, greater kudu and carnivores including African wild dog, lion and leopard (Hofer et al., 2004). Conversely, a small degree of expansion of woodlands (closed and open) is projected into wetter areas, for instance, into the Lake Tanganyika, Victoria and Pangani basin (Figure 7). However, there are predicted severe losses (over 40% by 2085 even under optimistic conditions) (Table 8) in suitable habitat for thickets in central and north-eastern Tanzania in the regions around Singida, Dodoma and Manyara (Figure 6c). Habitat fragmentation and reduced ecological resilience are anticipated, impacting the vital ecosystem for several game reserves and national parks with regionals and even global significance, including Mkungunero, Swagaswaga, Muhezi, Rungwa, Maswa, Mkomazi, Saadani, the Serengeti national park ecosystem and bee reserves in Manyoni District. These forest communities represent vital habitats for fauna such as birds, small browsers and larger animals such as rhinoceros, particularly in dry regions where thickets represent the only closed-canopy habitat (Medley & Hughes, 1996; Sharam, Sinclair, & Turkington, 2006).

Mangrove forests represent a valuable economic resource for local communities as well as maintaining the seascape. Importantly, mangrove forests play an essential role in carbon storage (natural

TABLE 6 Independent variables and their explanatory contributions to the distribution of the forests. It indicates habitat suitability changes within the range of the predictor variables. See Appendix 1 as Table A1 for a definition of the soil types

Forest type	Variable name	Unit	%	Mean	*SD*	Min.	Max.
Montane	Rainfall driest month	mm	59.8	14.80	0.64	0.00	66.00
	Terrain ruggedness	m	14.1	92.11	1.94	8.38	229.88
	Soil type (Nitisols, Histosols,)	-	8.6	-	-	-	-
	Potential evapotranspiration	mm	8.1	1,387.70	127.69	1,051.00	1791.00
	Mean annual temperature	°C	6.2	17.01	0.10	10.40	26.10
	Annual moisture index	-	1.2	90.74	22.51	47.00	209.00
	Mean annual rainfall	mm	1.0	1,247.61	10.72	850.00	2,686.00
	Elevation	m	0.5	1,760	19	235	3,039
	Rainfall wettest month	mm	0.4	232.18	65.15	143	514.00
Lowland	Rainfall driest month)	mm	49.8	11.20	0.33	0.00	56.00
	Elevation	m	21.7	363.32	7.34	9.00	2,377.00
	Terrain ruggedness	m	12.5	36.40	1.20	1.12	279.25
	Soil type (Arenosols, Fluvisols)	-	4.6	-	-	-	-
	Mean annual rainfall	mm	4.3	1,219.44	6.47	610.00	2,735.00
	Potential evapotranspiration	mm	3.3	1606.03	111.83	1,385	1787
	Annual moisture index	-	1.5	76.46	19.83	48.00	130.00
	Mean annual temperature	°C	1.2	24.72	0.04	15.00	27.30
	Rainfall wettest month	mm	1.1	223.05	58.65	150.00	405
Mangrove	Mean annual temperature	°C	21.0	26.69	0.04	25.90	27.50
	Elevation	m	72.0	8.82	0.08	1.00	22.00
	Soil type (Solonchanks, Arenosols)	-	2.8	-	-	-	-
	Terrain ruggedness	m	2.5	2.60	0.06	0.12	2,479.80
	Potential evapotranspiration	mm	1.3	1502.64	67.23	1,388.00	1791.00
	Rainfall wettest month	mm	0.3	297.59	66.62	154.00	467.00
	Mean annual precipitation	mm	0.1	1,342.84	4.46	992.00	1869.00
	Annual moisture index	-	0.0	89.93	13.77	56.00	135.00
	Rainfall driest month	mm	0.0	17.00	0.15	7.00	49.00
Closed woodland	Mean annual precipitation	mm	40.0	1,139.84	1.16	556.00	2,377.00
	Terrain ruggedness	m	14.2	29.96	0.16	0.38	248.12
	Rainfall wettest month	mm	11.7	215.98	48.38	111.00	359.00
	Mean annual temperature	°C	9.0	22.56	0.01	13.7	27.20
	Elevation	m	7.1	1,040.06	2.00	14.00	2039.00
	Soil type (Acrisols, Ferralsols)	-	7.1	-	-	-	-
	Rainfall driest month	mm	6.8	1.64	0.01	0.00	35.00
	Potential evapotranspiration	mm	2.5	1626.70	14.65	1,365	1869
	Annual moisture index	-	1.6	71.87	17.65	40	126

(Continues)

TABLE 6 (Continued)

Forest type	Variable name	Unit	%	Mean	*SD*	Min.	Max.
Open woodland	Rainfall driest month	mm	41.7	3.59	0.04	0.00	48.00
	Terrain ruggedness	m	27.0	22.88	0.21	0.25	231.12
	Soil type (Ferralsols, Gleysols)	-	18.2	-	-	-	-
	Mean annual precipitation	mm	8.3	766.08	11.45	566.00	1,243.00
	Annual moisture index	-	1.7	62.44	15.87	24.00	114.00
	Elevation	m	1.3	942.05	3.54	10.00	2,276.00
	Rainfall wettest month	mm	0.9	187.25	44.80	66.00	308.00
	Potential evapotranspiration	mm	0.5	1657.27	101.82	1,409.00	1,890.00
	Mean annual temperature	°C	0.3	22.97	0.01	13.90	27.30
Thicket	Mean annual precipitation	mm	32.5	766.08	11.45	566.00	1,243.00
	Soil type (Acrisols and Arenosols)	-	27.3	-	-	-	-
	Terrain ruggedness	m	13.1	8.78	0.67	2.38	45.38
	Rainfall driest month	mm	12.3	3.27	0.80	0.00	38.00
	Rainfall wettest month	mm	7.4	144.09	17.03	114.00	219.00
	Annual moisture index	-	6.2	44.93	7.91	32.00	75.00
	Potential evapotranspiration	mm	0.9	1707.40	55.27	1,580.00	1891.00
	Elevation	m	0.1	1,160.47	28.57	106.00	1516.00
	Mean annual temperature	°C	0.1	22.19	0.10	20.10	25.60

carbon sinks), capturing CO_2 from the atmosphere and store it in their biomass than terrestrial trees (Alongi, 2012; Ray & Jana, 2017). Under projected climate change scenarios, habitats suitable for mangrove forests are predicted to expand their range by 40% (Tables 7 and 8) at both low and high emissions (Figure 8). It is chiefly due to rising temperatures and subsequent evaporation, coupled with reduced annual rainfall totals leading to increased salinity, a favourable condition for mangrove ecosystem (Alongi, 2015). Therefore, an increase in temperature would be positive to the mangrove ecosystem as more accelerated growth, changes in community composition, diversity and latitudinal expansion (Alongi, 2015; Hanebuth, Kudrass, Linstädter, Islam, & Zander, 2013). Similarly, a rise in sea level influenced by future climate change is expected to alter mangrove forests significantly as they are susceptible to any shift in sea level (Alongi, 2008; Crase, Vesk, Liedloff, & Wintle, 2015). The relative sea-level rise may cause landward retreat in mangrove forests supported by sediment composition on the upland habitat (Godoy & Lacerda, 2015).

5.3 | Implications for forests conservation planning

A dramatic decline in the projected extent of Tanzanian forests over the next 50 years is expected to be driven by regional and national climatic factors. Our study, therefore, identifies a tractable method of using existing forest inventory data to predict the distribution of future habitats capable of sustaining forest ecosystems in spite of the challenges posed by future climate change. Information on forest extent and change of this nature can directly inform schemes such as the Clean Development Mechanism (CDM) and REDD+ (Pelletier & Goetz, 2015) as an incentive and alternative plans to reduce pressure to the remaining suitable forest habitats and enhance forest conservation, sustainable forest management and enhancement of forest carbon stocks and payment of ecosystem services (Romijn et al., 2012).

The habitat modelling procedure demonstrated that climate has a substantial control on the distribution of Tanzanian forest communities. As a result, even under an optimistic climate change scenario (RCP4.5), forest communities in Tanzania are projected to decrease in an immense range. Notably, montane forests of Tanzania are globally significant in terms of biodiversity (Fjeldså, 1999; Jones et al., 2012; Rovero et al., 2006), yet they are projected to halve in extent by 2085. Although forest communities like closed, open woodland, and mangrove forest may expand into other regions in response to climate change, montane forests are constrained by elevation and therefore show particular vulnerability to changes in temperature. As such, montane species may well act as a barometer for regional climate change (e.g. Kimball & Weihrauch, 2000). Focusing on monitoring efforts in these regions may be vital in identifying changes in forest composition and biodiversity in response to climate change, in the hope that this can steer policy before we reach a crucial tipping point. For instance, through efforts like the African Forest Landscape Restoration initiatives (FLR) with a target of restoring 100 million hectares of deforested and degraded landscape across Africa by 2030 (Mills et al., 2015).

Other more direct anthropogenic factors compound the threat from climate change as these forest communities undergo extensive

TABLE 7 Predicted changes in forests habitat in km^2 and percentage (%) from the baseline for RCP4.5 (2055) and RCP4.5 (2085)

	Baseline		RCP4.5—2055				RCP4.5—2085			
Forest type	Suitable	Not suitable	Loss	Gain	Suitable	Not suitable	Loss	Gain	Suitable	Not suitable
Closed woodland	450,151	484,756	14,319 (3.18)	15,026 (3.34)	435,832	469,730	22,061 (5.00)	11,608 (2.58)	428,090	473,148
Open woodland	662,595	272,312	16,676 (2.52)	13,145 (2.00)	645,919	259,167	24,088 (3.64)	16,989 (2.56)	638,507	255,323
Montane forest	58,019	876,888	23,619 (40.70)	133 (0.24)	34,400	876,755	27,400 (47.22)	119 (0.20)	30,619	876,769
Mangrove forest	1,467	933,442	319 (21.75)	652 (44.44)	1,148	932,790	222 (15.13)	681 (46.42)	1,245	932,761
Lowland forest	117,178	817,731	3,872 (3.30)	9,849 (8.40)	113,306	807,882	4,810 (4.10)	10,198 (8.70)	112,368	807,533
Thicket	172,662	762,245	0 (0)	0 (0)	177,881	757,026	65,061 (37.68)	3,729 (2.15)	107,601	758,516

TABLE 8 Predicted changes in forests habitat in km^2 and percentage (%) from the baseline for RCP8.5 (2055) and RCP8.5 (2085)

	Baseline		RCP8.5—2055				RCP8.5—2085			
Forest type	Suitable	Not suitable	Loss	Gain	Suitable	Not suitable	Loss	Gain	Suitable	Not suitable
Closed woodland	45,0,151	484,756	17,951 (4.00)	9,625 (2.14)	432,200	475,131	15,066 (3.35)	16,681 (3.71)	435,085	468,075
Open woodland	662,595	272,312	26,710 (4.03)	9,039 (1.36)	635,885	263,273	20,420 (3.08)	18,145 (2.74)	518,376	254,167
Montane forest	58,019	876,888	28,827 (49.68)	114 (0.19)	29,191	876,774	37,343 (64.36)	128 (0.22)	20,676	876,760
Mangrove forest	1,467	933,442	199 (13.56)	714 (48.67)	1,268	932,728	257 (17.51)	626 (42.67)	1,210	932,816
Lowland forest	117,178	817,731	7,746 (6.61)	8,011 (6.84)	109,432	809,720	11,891 (10.15)	7,377 (6.30)	105,287	810,354
Thicket	172,662	762,245	70,589 (40.88)	3,256 (1.88)	102,073	758,989	127,588 (73.89)	1,267 (0.73)	45,074	760,978

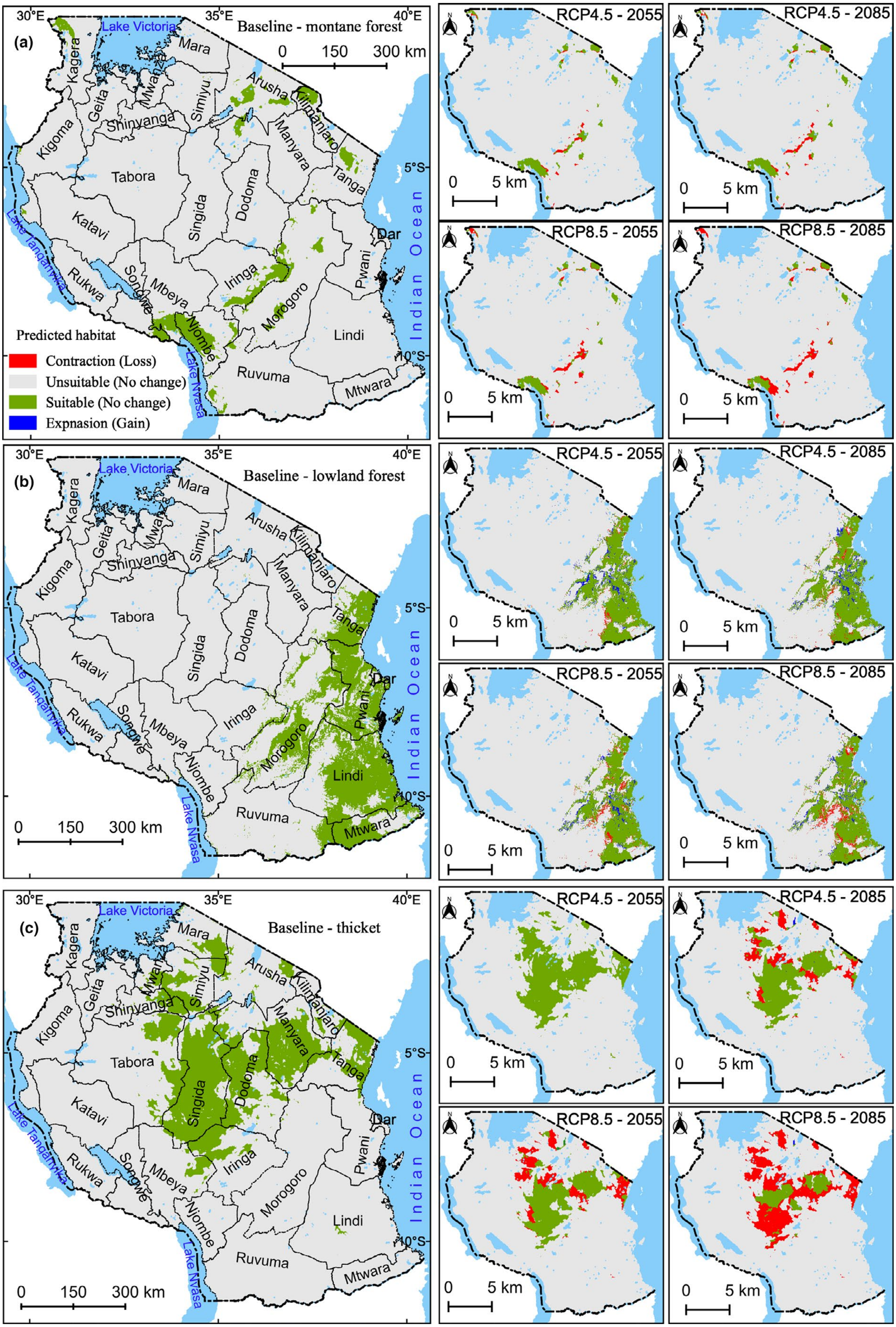

FIGURE 6 Predicted spatial changes in the potential habitat distribution area based on the thresholds provided in Table 4 for (a) montane (b) lowland forest (c) thicket under current and future climate scenarios. EPSG: 4,326, WGS84 projection

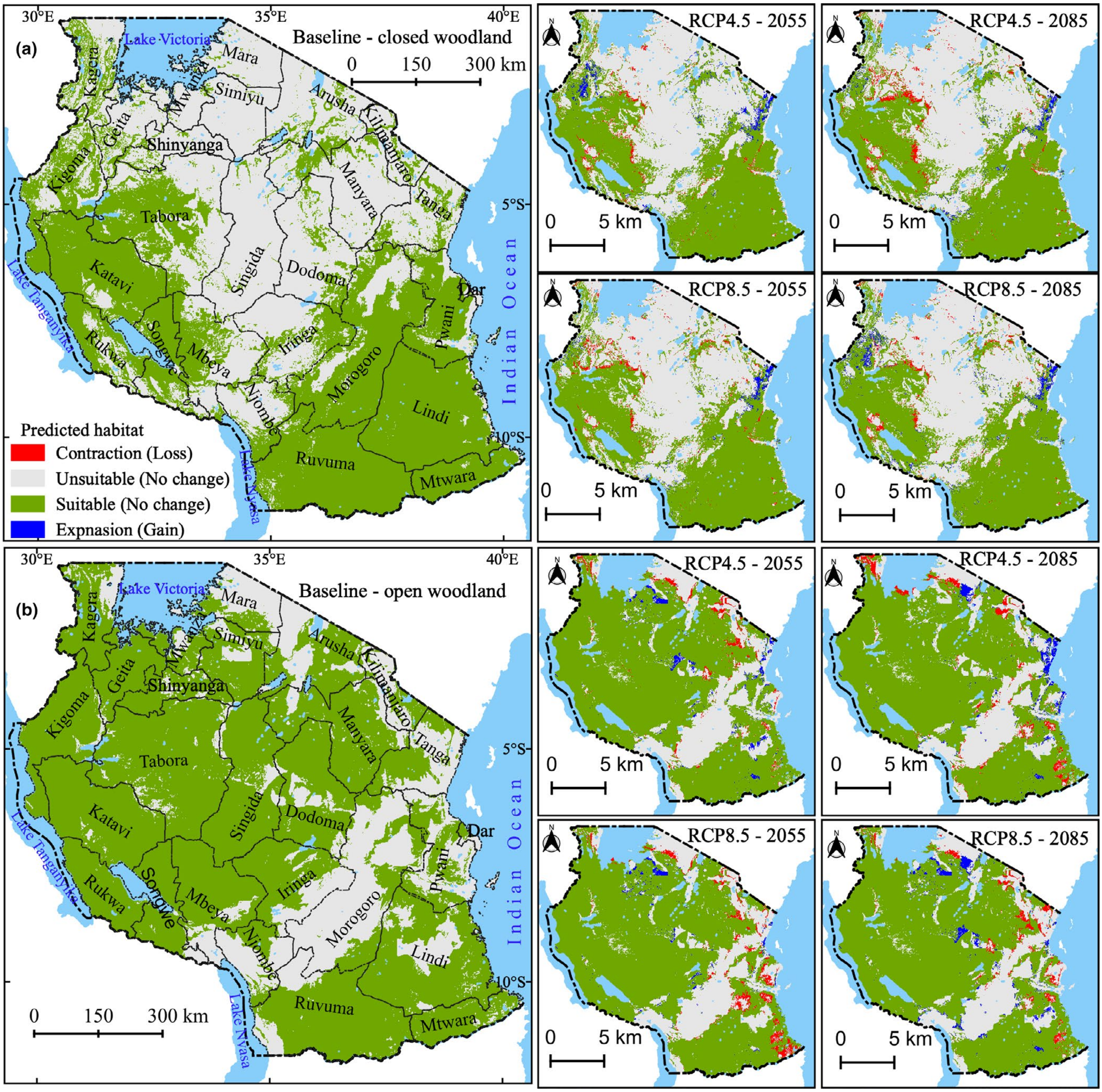

FIGURE 7 Predicted spatial changes in the potential habitat distribution area based on the thresholds provided in Table 4 for (a) closed woodland (b) open woodland under current and future climate scenarios. EPSG: 4,326, WGS84 projection

felling for building material and charcoal production, as well as increasing frequency of forest fires (Sharam et al., 2006). These forest habitats extend across approximately half of Tanzania, and habitat degradation or loss of this magnitude can have serious implications, particularly in terms of loss of carbon sink (Makundi & Okiting'ati, 1995) and their role in wildlife migratory patterns: projected losses coincide with wildlife corridors with regional significance such as the Selous-Niassa, Udzungwa-Ruaha and Muhezi-Swagaswaga migratory routes (Hofer et al., 2004; Medley & Hughes, 1996; Sharam et al., 2006).

5.4 | Limitations of the study

This study adopted a widely accepted methodology (e.g. Elith et al., 2006; Lim et al., 2018; Merow et al., 2013) that facilitates mapping of forests habitat suitability and their alteration due to climate change; however, it suffers from the same limitations associated with known uncertainties of the data and climate models (e.g. Watling, Brandt, Mazzotti, & Romañach, 2013). Similarly, the forest habitats prediction focused at a county level, and therefore, our results should be interpreted at the national scale rather than a regional or small local scale.

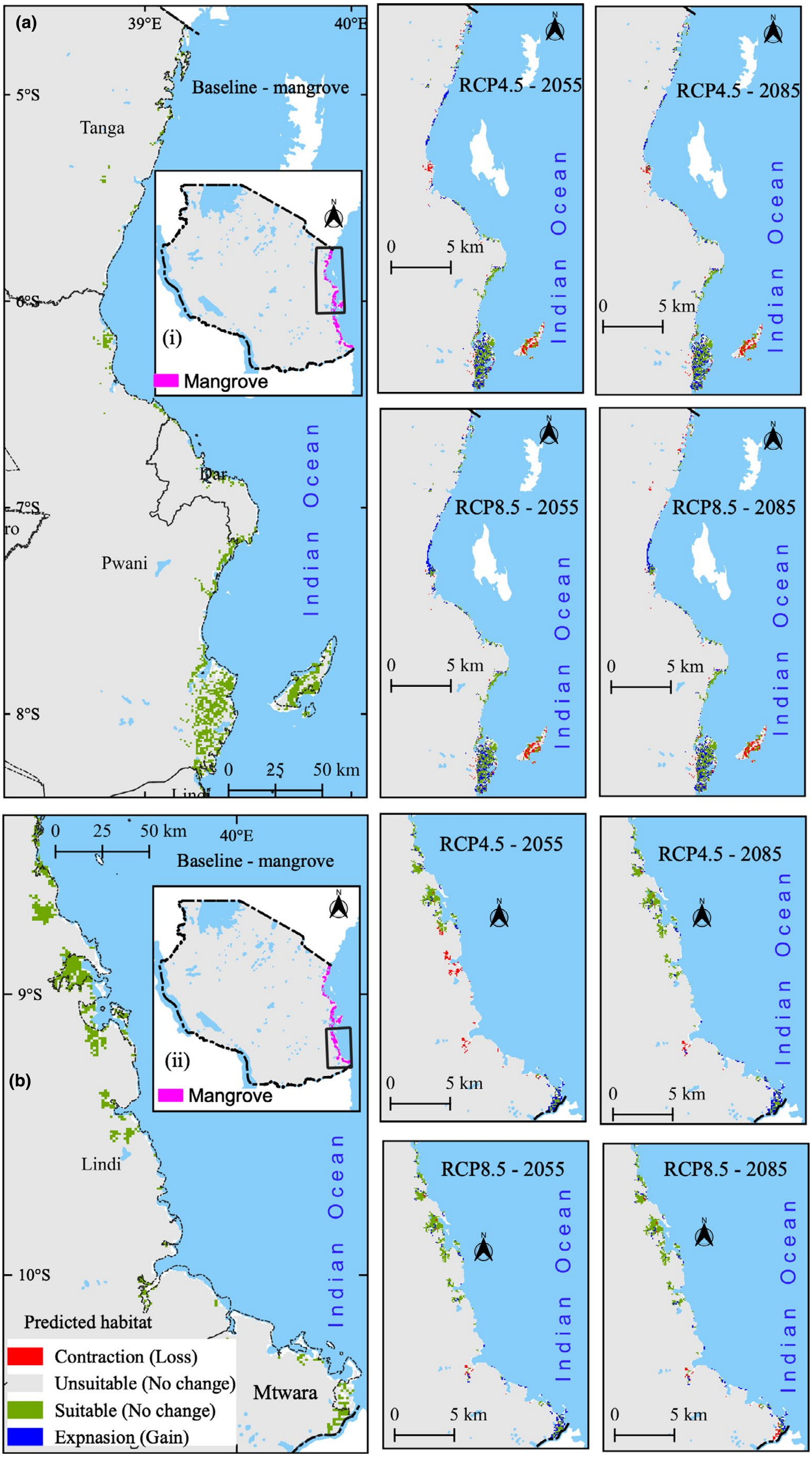

FIGURE 8 Predicted spatial changes in the potential habitat distribution area of mangrove under current and future climate scenarios based on the thresholds provided in Table 4: (a) northern coastline of Tanzania (b) southern coastline of Tanzania. EPSG: 4,326, WGS84 projection

5.5 | Future research perspectives

Future simulations should consider using the information on the spatial pattern of change, such as proximity (distance rasters) to urban centres and road networks, and density rasters of projected population growth (population data surface). Construction of road networks across forests is likely to trigger increased forest degradation and fire incidences that in turn are expected to alter regional climate (Fonseca et al., 2019; Nepstad et al., 2001). Future work also should explicitly consider the impact of sea-level rise and geomorphology on Tanzanian mangroves to fully understand how these essential habitats might change as a result of climate change.

5.6 | Conclusions

Climate change will alter Tanzanian forests by accelerating habitat loss, fragmentation and hence reducing ecological connectivity. The effect of forest fragmentation will compromise the potential plant pollinators' movement and seed dispersal. The induced fragmentation is especially severe when essential wildlife corridors, such as riparian zones that connect different areas of the landscape, are impacted. The optimal management solution in this regard is to increase ecological connectivity in current forest planning and management. Ecological connectivity should be maintained in habitats that are predicted not to change and expand under future climate change by preserving native forests and, where possible, protect the remaining forest areas from other anthropogenic disturbances. Improving ecological connectivity would significantly enhance not only sustainable forest management but also improve the design and implementation of forest projects and programmes. For example, ecological connectivity in forests will improve wildlife movement. This is more prominent for the dispersed population of large mammals (e.g. elephants) (Ntongani et al., 2010), when enclosed, increase the destructions of the highly diverse forest habitats (Ripple et al., 2015). Therefore, increasing forest connectivity will enhance the natural resilience of the remaining forests to the predicted effects of climate change. Consequently, the findings call for conservation planning in different dimensions: improve management of the existing protected areas which can absorb the impact of climate change, but also expanding to newly suitable areas with effective land use planning, conservation and land reclamation.

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PEER REVIEW

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DATA AVAILABILITY STATEMENT

The datasets for this study are available from the corresponding author upon request.

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BIOSKETCH

Our research at the Earth Observation and Ecosystems Dynamics Laboratory focuses on the integration of ground, airborne and space-borne remote sensing data for better understanding the direct and indirect impacts of anthropogenic activities and climate change on ecosystems and environments (https://www.aber.ac.uk/en/dges/research/earth-observation-laboratory).

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APPENDIX 1

TABLE A1 Summary of dominant soil groups in Tanzania (Batjes, 2004)

Code	Major soil group	Descriptions
1	Acrisols	Strongly weathered acid soils, with low base saturation
2	Andosols	Black soils of volcanic landscapes, rich in organic matters
3	Arenosols	Sandy soils with limited soil development, under scattered (mostly grassy) vegetation to very old plateaus of light forest
4	Cambisols	Weakly to moderately developed soil soils occurring from seal level to the highlands and under all kind of vegetation (savanna woodland and forests)
5	Chernozems	Black soil rich in organic matter, occurring in flat to undulating plains with forest and tall grass vegetation
6	Ferralsols	Deep, strongly weathered, physically stable but chemically depleted
7	Fluvisols	Associated with important river plains, periodically flooded areas
8	Gleysols	Temporary or permanent wetness near soil surface, support swamp forests or permanent grass cover
9	Histosols	Peat and muck soils with incompletely decomposed plant remains
10	Leptosols	Shallow soils over hard rock/gravel, at medium to high altitude landscapes, suitable for forestry and nature conservation
11	Lixisols	Strongly weathered and leached, finely textured materials support natural savanna or open woodland vegetation
12	Luvisols	Common in flat or gently sloping land with unconsolidated alluvial, colluvial, aeolian deposits in cooler environments and young surface
13	Nitisols	Deep, red, well-drained tropical soils with a clayey, well defined nut-shaped peds with shiny surface. Found in level to highland under tropical rain forest or savanna vegetation
14	Phaeozems	Dark soils, rich in organic matter. Occur on flat to undulating land in a warm to cool (tropical highland). Support natural vegetation with tall grass steppe and or/forest
15	Planosols	Clayey alluvial and colluvial deposits and support light forest or grass vegetation
16	Regosols	Contain gravelly lateritic materials (murrum) with low suitability for plant growth
17	Solonchanks	Occur in seasonally or permanently water logged areas with grasses and/or halophytic herbs
18	Solonetz	Associated with flat lands in a hot climate, dry summers, coastal deposit. Contain a high proportional of sodium ions
19	Vertisols	Contain sediments with a high proportion of smectite clay, high swelling and shrinking of results in deep cracks during dry season. Climax vegetation is savanna, natural grass and/or woodland
20	Water body	-

TABLE A2 Environmental variables are based on the 3-PG model; bold abbreviated variables are used in the final model after testing for collinearity using a pairwise Pearson correlation

Variable name	Explanation	Unit
PET seasonality (PETseason)	Monthly variability in potential evapotranspiration	mm/month
PET Warmest Quarter (PETWarmQ)	Mean monthly PET of warmest quarter	mm/month
PET wettest quarter (PETWetQ)	Mean monthly PET of wettest quarter	mm/month
Thermicity index (ThermicitI)	Sum of mean annual temp., min. temp. of the coldest month, max. temp. of the coldest month, x 10, with compensations for better comparability across the globe	°C
Elevation (**Elv**)	Height above or below sea level	m
Terrain ruggedness index (**Tri**)	Calculates the difference in elevation values from a centre cell and the eight cells immediately surrounding it	m
Topographic wetness index (TopoWet)	This quantifies topographic control on the hydrological process	-
Soil water availability capacity (SoilwaterA)	Plant available water holding capacity (v%) of the soil	mm
Soil types (**ST**)	Characterized by a variety of textures and nutrients	-
Potential evapotranspiration (**PET**)	Amount of evaporation taking place when sufficient water is available	mm
Mean annual temperature (**Bio1**)	The average temperature for each month	°C
Mean annual rainfall (**Bio12**)	This is the sum of all total monthly precipitation values	mm
Rainfall wettest month (**Bio13**)	This index identifies the total rainfall that prevails during the wettest month	mm
Rainfall driest month (**Bio14**)	This index determines the total precipitation that prevails during the driest month	mm
Annual moisture index (**Mi**)	Mean annual rainfall/Potential evapotranspiration	-

TABLE A3 Correlation matrix between environmental predictors and variables with high correlation are shown with r > 0.7 or < −0.7 in bold at a significance level of .01 (see Table A2 for the details of abbreviations)

	Tri	TopoWet	Elv	ThermicitI	Bio1	PET	PETWetQ	PETWarmQ	PETseason	Mi	Bio14	Bio13	Bio12	ST	Soilwater
Tri	1														
TopoWet	**−0.795**	1													
Elv	0.325	−0.423	1												
ThermicitI	−0.441	0.572	**−0.862**	1											
Bio1	−0.426	0.553	−0.205	0.473	1										
PET	−0.324	0.422	−0.046	0.401	0.38	1									
PETWetQ	−0.282	0.333	0.005	0.298	0.289	**0.896**	1								
PETWarmQ	−0.257	0.317	−0.007	0.297	0.28	**0.916**	**0.853**	1							
PETseason	0.115	−0.16	−0.222	−0.041	0.009	**−0.74**	0.058	0.211	1						
Mi	0.235	−0.304	−0.124	−0.073	−0.061	−0.31	−0.43	−0.627	0.013	1					
Bio14	0.101	−0.049	−0.336	0.138	0.151	−0.163	−0.333	−0.172	0.209	0.249	1				
Bio13	0.152	−0.205	−0.208	0.075	0.092	−0.522	−0.55	−0.409	0.157	0.007	0.201	1			
Bio12	0.177	−0.234	−0.18	0.052	0.059	−0.545	−0.618	−0.477	−0.021	0.073	0.249	0.025	1		
ST	0.325	−0.347	0.482	−0.409	−0.414	−0.001	0.008	0.010	−0.111	−0.023	−0.115	−0.051	−0.035	1	
Soilwater	0.198	−0.22	0.258	−0.237	−0.243	−0.135	−0.17	−0.11	−0.117	**0.709**	−0.049	0.196	0.259	0.154	1